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Crangonyx islandicus sp. nov., a subterranean freshwater amphipod (Crustacea, Amphipoda, Crangonyctidae) from springs in lava fields in Iceland

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Abstract

Crangonyx islandicus **sp. nov.** (Crustacea, Amphipoda, Crangonyctidae) is described from Iceland. This is the second species of freshwater, subterranean, gammaridean amphipods found in Iceland and the first species of the family Crangonyctidae. *Crangonyx islandicus* **sp. nov.** can be distinguished from other species of the genus *Crangonyx* by combination of the following characters: the number of spines on the outer and inner lobes of the maxillipedal palp, the presence of a spine at the base of the unguis of the dactylus of gnathopods 1 and 2, stout and short uropod 3, and by a short and wide telson. The species was recorded in South, Southwest, West and Northeast Iceland from numerous springs emerging from relatively young (<10 000 years), porous lavas. The species has apparently survived Pliocene and Pleistocene glaciations in groundwater of porous lava fields and may have persisted in Iceland for several million years.

Key words: Amphipoda, *Crangonyx*, Crangonyctidae, Crangonyctoidea, Iceland, glaciations, subterranean, groundwater, subarctic

Introduction

Subterranean waters hold a variety of organisms of most animal phyla (see Botosaneanu 1986). Amphipods (Crustacea) are among the animals that characterise subterranean habitats world-wide, with more than 1000 amphipod species described from subterranean waters (Sket 1999). Due to the diversity of amphipods in subterranean waters and their long presence there, subterranean amphipods are excellent tools for evaluation of biogeographical patterns (Holsinger 1977, 1986, 1993).

Subterranean amphipods are rare at higher latitudes and only a few species have been

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described from subarctic Alaska and Siberia (Holsinger 1986). From northern Europe subterranean amphipods have only been reported from South England and Ireland (Costello 1993). Recently the new species of subterranean amphipod, *Crymostygius thingvallensis* Kristjánsson & Svavarsson, 2004, belonging to a new family, Crymostygiidae Kristjánsson & Svavarsson, 2004, was described from Iceland, in subarctic Europe (Kristjánsson & Svavarsson 2004). During an intensive search for *C. thingvallensis* another amphipod species was discovered and this species has later been collected at numerous springs in Southern, Southwestern, Western, and Northeastern Iceland, using electric fishing gear. Here, a description is given of the new species, and the possible origin of the species is discussed.

The type material is deposited at the Icelandic Museum of Natural History (IMNH), Reykjavík, Iceland.

Taxonomy

Crangonyctidae Bousfield, 1973 (emended 1977)

Genus *Crangonyx* Bate, 1859

Diagnosis (see Zhang & Holsinger 2003).

Crangonyx islandicus sp. nov.

(Figs 1–6)

Material examined

Holotype. Female, 6.8 mm, non-ovigerous, brood plates with setae, Vatnsvik, 64°14.46´N, 21°03.19´W, Thingvallavatn, Southwest Iceland, 12 July 2001, groundwater inflow to the lake, 4°C, 30 ppm conductivity, electric fishing, coll. B.K. Kristjánsson, IMNH 2164.

Paratypes. Vatnsvik, 64°14.46´N, 21°03.19´W, Thingvallavatn, Southwest Iceland, 8 May 2001, 21 specimens (drawn paratype included), groundwater inflow to the lake, electric fishing, coll. B.K. Kristjánsson, IMNH 2165; Vatnsvik, 64°14.46´N, 21°03.19´W, Thingvallavatn, Southwest Iceland, 12 July 2001, 7 specimens, groundwater inflow to the lake, electric fishing, coll. B.K. Kristjánsson, IMNH 2166; Nautavakir, 64°00.876´N, 20°53.018´W, Southwest Iceland, 1 August 2003, 6°C, 60 ppm conductivity, coll. B.K. Kristjánsson & J. Svavarsson, 1 specimen, IMNH 2167.

Other material examined

Vatnsvik (64°14.46´ N, 21°03.19´ W), Thingvallavatn, Southwest Iceland, electric

fishing, coll. B.K. Kristjánsson: 5 September 2000, 1 specimens; 6 September 2000, 6 specimens; 25 February 2001, 22 specimens; 31 March 2001, 18 specimens; 7 May 2001, 2 specimens; 21 May 2001, 27 specimens; 12 June 2001, 7 specimens; 25 July 2001, 42 specimens; 6 June 2002 (ethanol preserved), 10 specimens; 30 June 2003, 16 specimens. Skútavík, Thingvallavatn, Southwest Iceland, approximately 64°08.5´N, 21°02.5´W, electric fishing, coll. B.K. Kristjánsson, 2 specimens; Nautavakir, Grímsnes, Southwest Iceland, 64°00.876´N, 20°53.018´W, 7 June 2002, from the stomach of arctic charr (*Salvelinus alpinus*; 60.9 mm) fished in groundwater outflow, electric fishing, coll. B.K. Kristjánsson, 1 specimen, damaged; Spring at Gunnarsholt, South Iceland, 21 July 2004, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Keldur, spring at area 1, South Iceland, 63°49.346´N, 20°04.561´W, 21 July 2004, 2.9°C, 110 ppm conductivity, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Lind (spring close to Keldur), South Iceland, 63°49.607´N, 20°05.783´W, 21 July 2004, 3.8°C, 120 ppm conductivity, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Rangárbotnar, South Iceland, 22 July 2004, electric fishing, coll. B.K. Kristjánsson, 2 specimens; Galtalækur, South Iceland, 64°00.478´N, 19°55.113´W, 22 July 2004, 5°C, 110 ppm conductivity, electric fishing, coll. B.K. Kristjánsson, 6 specimens; Lækjarbotnar, area 1, South Iceland, 63°57.442´N, 20°15.923´W, 23 July 2004, 4.8°C, 70 ppm, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Lækjarbotnar, area 2, South Iceland, 63°57.442´N 20°15.923´W, 23 July 2004, 4.8°C, 80 ppm conductivity, electric fishing, coll. B.K. Kristjánsson, 79 specimens; Stóri Galtalækur, South Iceland, 64°00.968´N, 19°57.793´W, 24 July 2004, 6°C, 90 ppm conductivity, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Lake Myvatn, Northeast Iceland, groundwater inflow north of Brjánsnes, 3 September 2004, electric fishing, coll. Viktor Burkni Pálsson & Gísli Már Gíslason, 9 specimens; Fljót, Grenlækur, South Iceland, 63°44.939´N, 17°56.714´N, 6 July 2005, 6.1°C, 70 ppm, electric fishing, coll. B.K. Kristjánsson, 15 specimens; Spring no. 1 below Tröllahylur, Grenlækur, South Iceland, 63°43.902´N, 17°58.144´W, 6 July 2005, 6°C, 80 ppm, electric fishing, coll. B.K. Kristjánsson, 14 specimens; Spring no. 2 below Tröllahylur, Grenlækur, South Iceland, 63°43.876´N, 17°58.064´W, 6 July 2005, 6°C, 60 ppm, electric fishing, coll. B.K. Kristjánsson, few specimens; Hrosslækur, Grenlækur, South Iceland, 63°43.559´N, 17°59.218´W, 6 July 2005, 5.8°C, 60 ppm, electric fishing, coll. B.K. Kristjánsson, few specimens; Spring south of the farm Höfði, Kirkjubær, South Iceland, 63°46.165´N, 18°04.368´W, 7 July 2005, 6.3°C, 70 ppm, electric fishing, coll. B.K. Kristjánsson, 2 specimens; Spring in the land of Hunkubakki, Kirkjubær, South Iceland, 63°45.705´N, 18°07.484´W, 7 July 2005, 4.8°C, 70 ppm, electric fishing, coll. B.K. Kristjánsson, 2 specimens; Spring near Klausturlax, Kirkjubær, South Iceland, 63°46.906´N, 18°03.013´W, 7 July 2005, 5.9°C, 70 ppm, electric fishing, coll. B.K. Kristjánsson, 15 specimens; Springs at Þverá, South Iceland, 63°52.423´N, 17°49.231´W, 9 July 2005, 7.3 and 6.2°C, 40 ppm, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Oddar, Húsafell, West Iceland, 64°42.132´N, 20°53.805´W, 27 July 2005, 4.2°C, 20 ppm, electric fishing,

coll. B.K. Kristjánsson, 1 specimen; Hrauná, Húsafell, West Iceland, 64°42.339´N, 20°59,721´W, 28 July 2005, 4.8°C, 30 ppm, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Sandur, Aðaldalur, Northeast Iceland, 65°57.241´N, 17°32.718´W, 7 September 2005, 5°C, 100 ppm, electric fishing, coll. B.K. Kristjánsson, 1 specimen; Klapparárá, Öxarfjörður, Northeast Iceland, 8 September 2005, 5°C, 50 ppm, electric fishing, coll. B.K. Kristjánsson, few specimens; Presthólar, Öxarfjörður, Northeast Iceland, 66°15.495´N, 16°24.123´W, 8 September 2005, 4.8°C, 60 ppm, electric fishing, coll. B.K. Kristjánsson, 1 specimen.

Diagnosis

Small size species distinguished by following characters: indication of eye pigment; mandibular palp segment 3 with 4 long plumose E-setae, row of 13 or more short bifid D-setae and 1 long B-seta; maxilla 2 inner plate with about 8 strong plumose setae in oblique row; maxilliped outer plate apically with 1 spine, 1 naked seta and 1 comb-like seta, inner margin with numerous naked setae; maxilliped inner plate somewhat truncated, apically with 6 plumose setae, naked seta laterodistally, single strong spine on mediodistal corner and medial margin with about 6 plumose setae; gnathopod 1 propodus palmar margin with few bifid spines, defining angle shallow, not distinct, with 6 lateral bifid spines, largest in middle, posterior ones reaching lateral corner, medially 7 short spines, dactylus with spine at base of unguis; gnathopod 2 propodus longer than propodus of gnathopod 1, palmar margin with defining angle shallow, not distinct, with 5 bifid setae on each side, dactylus with spine at base of unguis; uropod short; peduncle short and wide, 2 small naked setae on medial margin, inner ramus vestigial, about 50 % of peduncle length and about 35 % of length of outer ramus, outer ramus 1-segmented, two pairs of spines on lateral margin, two spines on medial margin; 4 apical spines; telson width 68 % of length, apical margin cleft, cleft about 29 % length of telson; apical lobes with 1–2 spines each; stalked, club shaped coxal gills on gnathopod 2 and pereopods 3 to 6, sternal gills/processes absent.

Description of females

Body length (non-ovigerous) 6.0 to 6.9 mm (N = 10) (Fig. 1). Body short and wide, unpigmented. Indication of eye pigment (clearly visible in life specimens). Pleonites and uronites with several fine setae dorsally. Uronites unfused. Interantennal lobe of head narrowly rounded anteriorly, inferior antennal sinus moderately deep. Coxal plates deep, overlapping; increasing in depth from pereonite 1 to 3; coxal plate 4 large, about as long as wide, posterior margin widely concave. Coxal plates 5 to 7 decreasing in size towards coxal plate 7; plate 5 bilobed; plate 6 with posterior end deeper, plate 7 small. Distoposterior corners of pleonal plates 1 and 2 angular, pleonal pate 3 evenly rounded, single seta on posterior margin.

Antenna 1 (Fig. 2A) long, about 70 % length of body; second peduncle segment 74 % of length of first peduncular segment; third peduncular segment 71 % of length of second

peduncular segment; primary flagellum with about 29–30 segments; aesthetascs on most segments, most often 1 aesthetasc, sometimes 2 aesthetascs (Fig. 2B); accessory flagellum 2-segmented (Fig. 2C); first segment distally with 2 naked setae and 1 plumose seta; terminal segment short, with 1 naked seta.

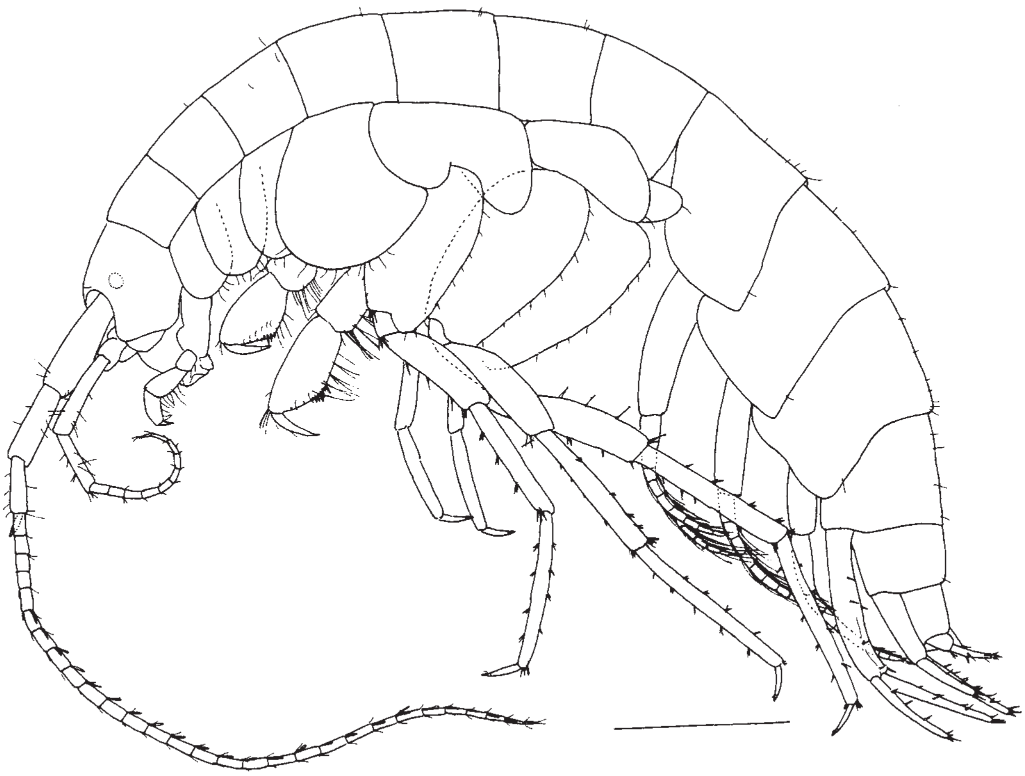

FIGURE 1. *Crangonyx islandicus* **sp. nov.**, female paratype, 6.2 mm, Vatnsvik. Habitus. Scale: 1 mm.

Antenna 2 (Fig. 2D) short, about 26 % of body length; 37 % of length of first antenna. Third peduncular segment about 92 % of length second peduncular segment. Flagellum with 9–10 segments.

Upper lip (Fig. 2E) slightly bilobed apically.

Mandible (Fig. 2F, G) well developed. Left lacina mobilis 5-dentate, incisor 5-dentate, about 8 large spines and some small in spine row; molar pointed, truncated distally, 1 long seta subapically. Palp with 3 segments (Fig. 2H), palp segment 2 with 7 naked setae on lateral margin, subequal to palp segment 3; palp segment 3 with 4 long plumose E-setae, row of 13 or more short bifid D-setae and 1 long B-seta.

Lower lip (Fig. 2I) with small setae on the margins of the outer lobes; mandibular lobes evenly rounded.

Maxilla 1 (Fig. 2J) inner plate with apical-medial row of about 16 plumose setae. Outer plate truncated, apically with 7 spines, medial margin of spines with numerous fine

denticles. Palp 2-segmented, article 2 apically with two comb-like setae, subapically naked setae.

Maxilla 2 (Fig. 2K) outer plate with two rows of setae; one row with about 11 faintly plumose setae, other row with about 8 faintly plumose setae. Inner plate with about 8 strong plumose setae in oblique row; apically two rows of setae, one with comb-like setae.

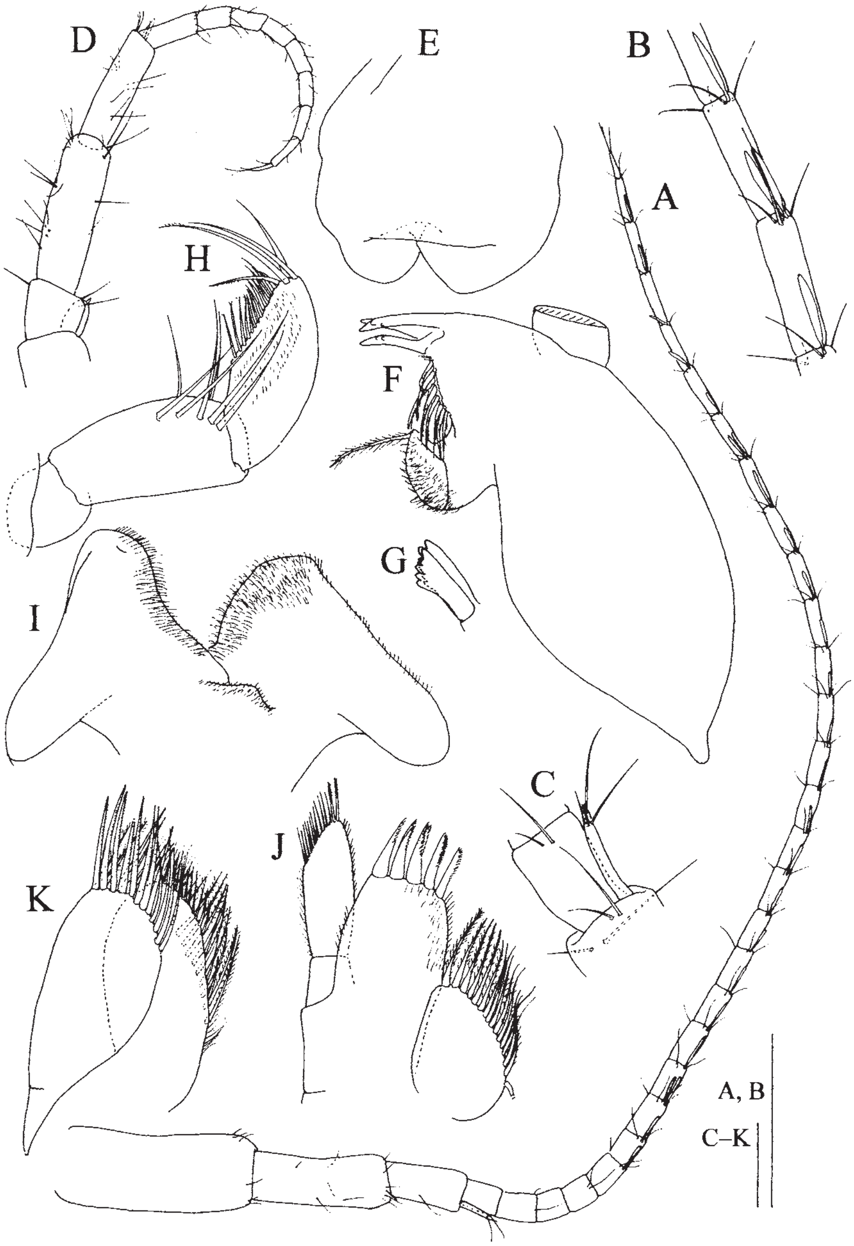

FIGURE 2. *Crangonyx islandicus* **sp. nov.**, female paratype, 6.2 mm, Vatnsvik. A, antenna 1. B, distal part of flagellum of antenna 1. C, accessory flagellum of antenna 1. D, antenna 2. E, upper lip. F, left mandible, G, lacina mobilis and incisor. H, mandibular palp. I, lower lip. J, maxilla 1. K, maxilla 2. Scale: A, B = 0.5; C–K = 0.1 mm.

Maxilliped (Fig. 3A). Outer plate (Fig. 3B) apically with 1 spine, 1 naked seta and 1 comb-like seta; inner margin with numerous naked setae. Inner plate (Fig. 3C) somewhat truncated, apically with 6 plumose setae, naked seta laterodistally, single strong spine on mediodistal corner; medial margin with about 6 plumose setae. Dactylus with fairly long, uncurved nail.

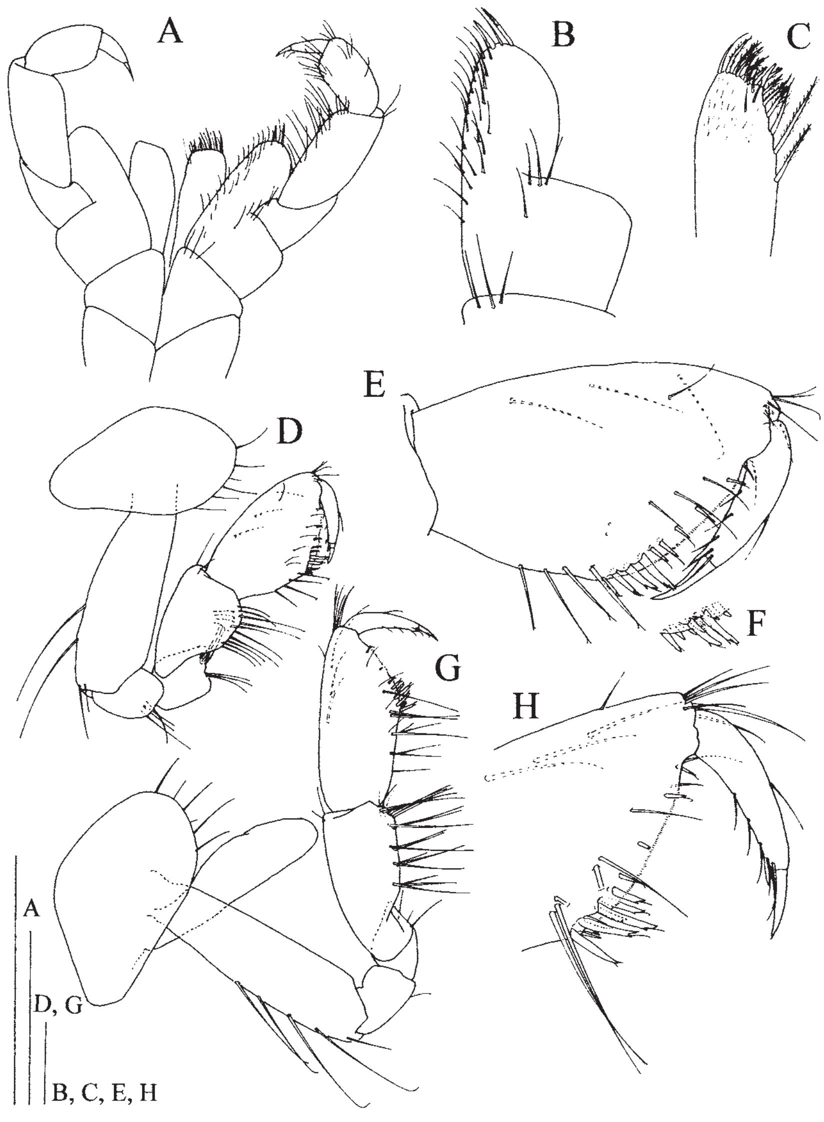

FIGURE 3. *Crangonyx islandicus* **sp. nov.**, female paratype, 6.2 mm, Vatnsvik. A, maxilliped. B, outer plate of maxilliped. C, inner plate of maxilliped. D, gnathopod 1. E, propodus and dactylus of gnathopod 1. F, short spines medially on gnathopod 1, in relation to largest two lateral bifid spines. G, gnathopod 2. H, distal part of propodus and dactylus of gnathopod 2. Scale: A = 0.5 mm; B, C, E, H = 0.5 mm; D, G = 0.1 mm.

Gnathopod 1 (Fig. 3D) short and stout; coxal plate somewhat longer than wide, with several setae distally; posterior margin of basis distally with few long setae; merus and ischium distally with cluster of naked setae; ischium ventrodistally produced, ventrodistally with few setae; carpus about 82 % of propodus length, with two rows of setae on posterior margin, few setae anterodistally; protopod shorter than protopod of gnathopod 2; propodus ovoid, palmar margin slightly oblique, margin finely serrate, with few bifid spines (Fig. 3E); defining angle shallow, not distinct, with 6 lateral bifid spines, largest in middle, posterior ones reaching lateral corner, medially 7 short spines (Fig. 3F); dactylus about 60 % of propodus length; few naked setae on posterior margin, dactylus with spine at base of unguis; unguis about 35 % of dactylus length.

Gnathopod 2 (Fig. 3G) slender, longer than gnathopod 1; coxal plate longer than wide, with several setae distally; basis longer than basis of gnathopod 1, posterior margin of basis distally with several long setae; ischium produced, posterodistally with few setae; carpus about 85 % of propodus length, with 4 rows of marginal setae with 3–4 setae in each row, posterodistally 7 setae in row; propodus longer than propodus of gnathopod 1, palmar margin slightly oblique, margin finely serrate (Fig. 3H), with 2 bifid spines and 2 naked setae near insertion of dactyl; defining angle shallow, not distinct, with 5 bifid setae on each side, setae on lateral side larger than setae on median side; posterior margin with rows of marginal setae, with increasing number of setae toward defining angle; dactylus about 50 % of propodus length, with few naked setae on posterior margin; dactylus with spine at base of unguis; unguis about 31 % of dactylus length.

Pereopods 3 and 4 (Figs 4A, B) slender, considerably longer than pereopod 2. Pereopod 4 slightly longer than pereopod 3; similar in number and placement of setae; pereopod 3 coxal plate longer than wide (width 62 % of length), with several setae distally; basis slender, longest article; carpus about 61 % of ischium length; propodus longer than carpus; propodus about 82 % of ischium length; dactylus about 33 % of propodus length, no spine at base of unguis; pereopod 4 coxal plate longer than wide (width 88% of length), with several setae distally, strongly concave posteriorly; basis slender, longest article; carpus about 65 % of ischium length; propodus longer than carpus; propodus about 82 % of ischium length; dactylus about 31 % of propodus length, no spine at base of unguis.

Pereopods 5–7 (Fig. 4C; 5A–C) longer than pereopods 3 and 4, similar in length; similar in number and placement of setae; pereopod 7 longest. Coxal plate of pereopod 5 large, bilobed, single seta on posterior end; coxal plates on pereopods 6 and 7 small; basis wide, posterior lobe well developed and overhanging; ischium stout, carpus more slender, longer than ischium; propodus longer than carpus; several stout bifid spines distally on carpus (Fig. 5D). Dactyl small, about 5 % propodus length, no spine at base of unguis.

Stalked, club shaped *coxal gills* present on gnathopod 2 and pereopods 3 to 6. Sternal gills/processes not observed. Broodplates present on gnathopod 2 and on pereopods 3–5.

Pleopods 1–3 (Fig. 5E–G) similar, biramous, unmodified; peduncle bearing 2 coupling spines. Pleopod 1 outer ramus with at least 8–9 free segments and fused segment

proximally, inner ramus with at least 7 segment and few fused segment proximally.

Uropod 1 (Fig. 6A) slender, peduncle with about 8 spines on dorsal surface. Rami subequal; inner ramus with 5 apical spines, 3 spines on mediodorsal surface, 2 spines on laterodorsal surface. Outer ramus with 5 apical spines; about 3 spines on laterodorsal surface.

Uropod 2 (Fig. 6B) about 67 % of length of uropod 1; peduncle with 2 spines dorsodistally. Outer ramus about 63 % of length of inner ramus, about as long as peduncle, with 5 apical spines and 3 spines on dorsal surface. Outer ramus with 5 apical spines, 5 spines on laterodorsaly, 5 spines mediodorsally.

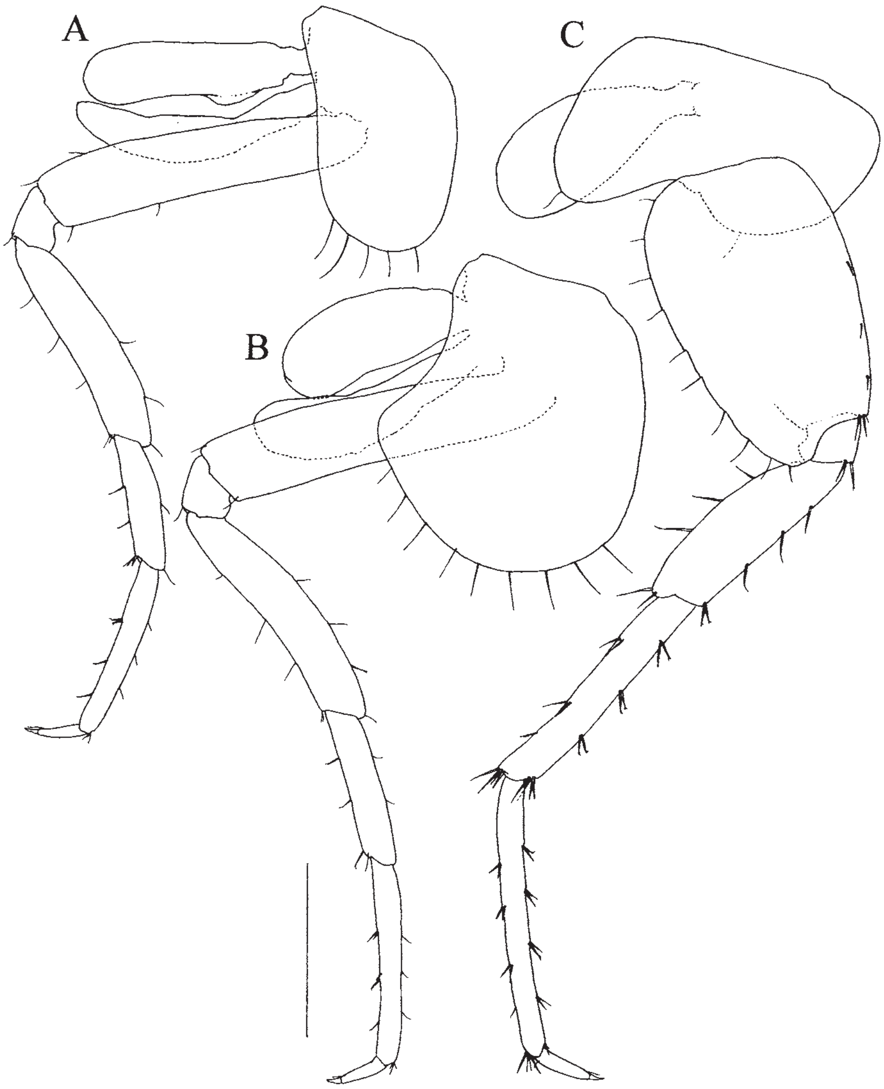

FIGURE 4. *Crangonyx islandicus* **sp. nov.**, female paratype, 6.2 mm, Vatnsvik. A, pereopod 3. B, pereopod 4. C, pereopod 5. Scale: 0.5 mm.

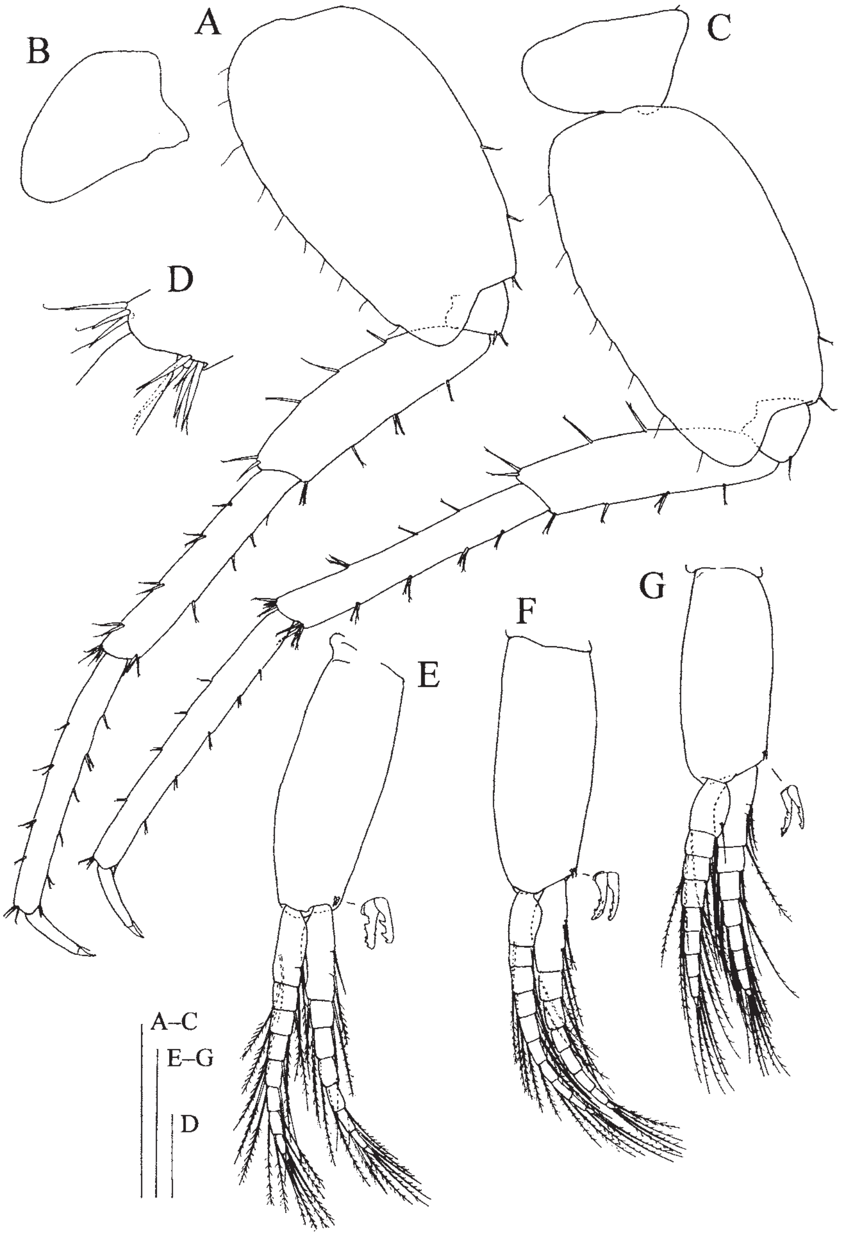

FIGURE 5. *Crangonyx islandicus* **sp. nov.**, female paratype, 6.2 mm, Vatnsvik. A, pereopod 6. B, coxa of pereopod 6. C, pereopod 7. D, spines distally on carpus of pereopod 7. E, pleopod 1. F, pleopod 2. G, pleopod 3. Scale: A–C = 0.5 mm; D = 0.1 mm; E–G = 0.5 mm.

Uropod 3 (Fig. 6C, D) short; peduncle short and wide, 2 small naked setae on medial margin; inner ramus vestigial, about 50 % of peduncle length and about 35 % of length of outer ramus; without seta. Outer ramus 1-segmented, flat and wide, two pairs of spines on lateral margin, two spines on medial margin; 4 apical spines.

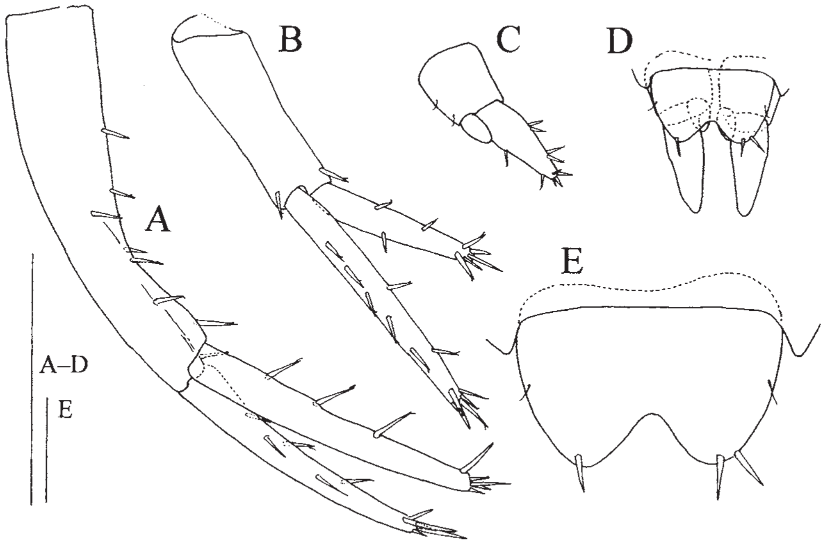

FIGURE 6. *Crangonyx islandicus* **sp. nov.**, female paratype, 6.2 mm, Vatnsvik. A, uropod 1. B, uropod 2. C, uropod 3. D, uropod 3 and telson. E, telson. Scale: A–D = 0.5 mm; E = 0.1 mm.

Telson (Fig. 6D, E) width about 68 % of length; apical margin cleft, cleft about 29 % length of telson; apical lobes with 1–2 spines each; lateral seta present.

Etymology

The name of the species refers to the country, where the species was sampled, i.e. Iceland. The gender is masculine.

Remarks

Most of the specimens were juveniles and females, having oostegites without setae. Only a few adult females were found. Adult males were not seen, and remain to be described.

The present species falls fairly well within genus *Crangonyx*. *C. islandicus* **sp. nov.**, however, does not appear to have sternal gills/processes, usually found on species of the genus *Crangonyx*. Furthermore, the presence of only a single strong spine on the inner plate of the maxilliped is unique within this genus. We hesitate to designate a new genus due to these small differences. Only a limited number of studies have focused on the function of the sternal gills, which are commonly found in freshwater amphipods. These may serve both in transporting as well as being respiratory organs (Kikuchi *et al.* 1993). Sternal gills may not be needed in the subterranean waters of Iceland, which are usually high in oxygen levels when not in direct contact with volcanic activity (S.R. Gíslason, pers. comm.), and can be very low in CO_2 contents (case shown in Gíslason *et al*. 1996).

The genus *Crangonyx* has recently been revised (Zhang & Holsinger 2003). The genus

contains 47 species, including the present one. *Crangonyx islandicus* **sp. nov.** can be distinguished from all other species of the genus by having only a single strong spine on the inner plate of the maxilliped. Other characteristics useful to distinguish the species from other species of the genus are: presence of a spine at the base of the unguis on gnathopods 1 and 2, relatively short uropod 3, wide telson with shallow notch and absence of sternal gills/processes. The morphological affinity of *C. islandicus* **sp. nov.** to the other species or species groups of the family remains unclear.

The species was collected at numerous springs in South, Southwest, West and Northeast Iceland (Fig. 7). At one of the spring inlets into Lake Thingvallavatn *C. islandicus* **sp. nov.** occurred together with the other stygobiont amphipod already known in Iceland, i.e. *Crymostygius thingvallensis* (Kristjánsson & Svavarsson 2004).

C. islandicus **sp. nov.** was always found at springs, but spring of various sizes, i.e. differing in the volume of the flowing water. Among the largest springs holding amphipods were those opening into Lake Thingvallavatn. The lake it self is about 90 % fed by groundwater (Adalsteinsson *et al*. 1992) and around 20 % of the groundwater inflow occurs at and nearby Vatnsvik, where *C. islandicus* **sp. nov.** has repeatedly been sampled. The site Rangárbotnar holds additionally extensive springs, being the origin of the large river Rangá, as well as the springs of Galtalækur. In some instances small springs were characterized by sand overlying the recent lava field, with groundwater pouring slowly from the spring.

At all sites the subterranean water was emerging from porous lava fields. The respective lava fields vary in age, but all areas are within the youngest part of the country (< 10 000 years old) (Fig. 7). The spring inlets sampling sites of Vatnsvik, South-western Iceland are located in the Eldborgir lava which has been dated to be of the age of 9130 ± 260 years (Kjartansson 1964; Sæmundsson 1992). The site Nautavakir is in the Grímsnes lavas, which are 5500–6500 years old (Jakobsson 1976). The site Lækjarbotnar and the sites at Galtalækur are all located in the Þjórsá lava. This is the most voluminous lava in Iceland, both in respect to flow and volume. This lava is considered to be 8580 ± 140 years old (Hjartarson 1988). The river Grenlækur has its origin in the Eldgjárhraun lava, which was formed around the year 934. However, the springs studied are located in the Landbrot lava, which has been dated 6200 ± 100 years before present (Jónsson 1987), although it has been suggested that the lava formed as late as in the 10th century (Larsen 1979). The youngest geological sites from which the species was recorded are those holding the springs at Þverá and the spring near the farm Hunkubakkar. These were located in the lava field Eldhraun, which was formed during the Skaftáreldar eruption in the year 1783.

The origin of the groundwater differs considerably between collecting sites, but remains still poorly recognised in many areas. The springs at Lake Thingvallavatn receive water from the ice cap of the glacier Langjökull. The water flows from the glacier presumably within 10 years to the site at Vatnsvik (Sveinbjörnsdóttir & Johnsen 1992). Many springs in the west of Iceland are known to be fed by the glacier Langjökull, while

springs in the north and the northeast are either feed by the large glacier Vatnajökull, or by local sources (surface rain draining through the porous lava), or mixture of both (Arnason 1976). The sampling site at Lake Myvatn receives groundwater from the local high grounds north of the lake (Einarsson *et al.* 2004).

The Icelandic groundwater differs from groundwater in other countries in having a high pH. It can be up to and above 10 before contact with the atmosphere (Gíslason *et al*. 1996). Consequently, the high pH can lead to direct pH enhancement of the dissolution rates of the minerals.

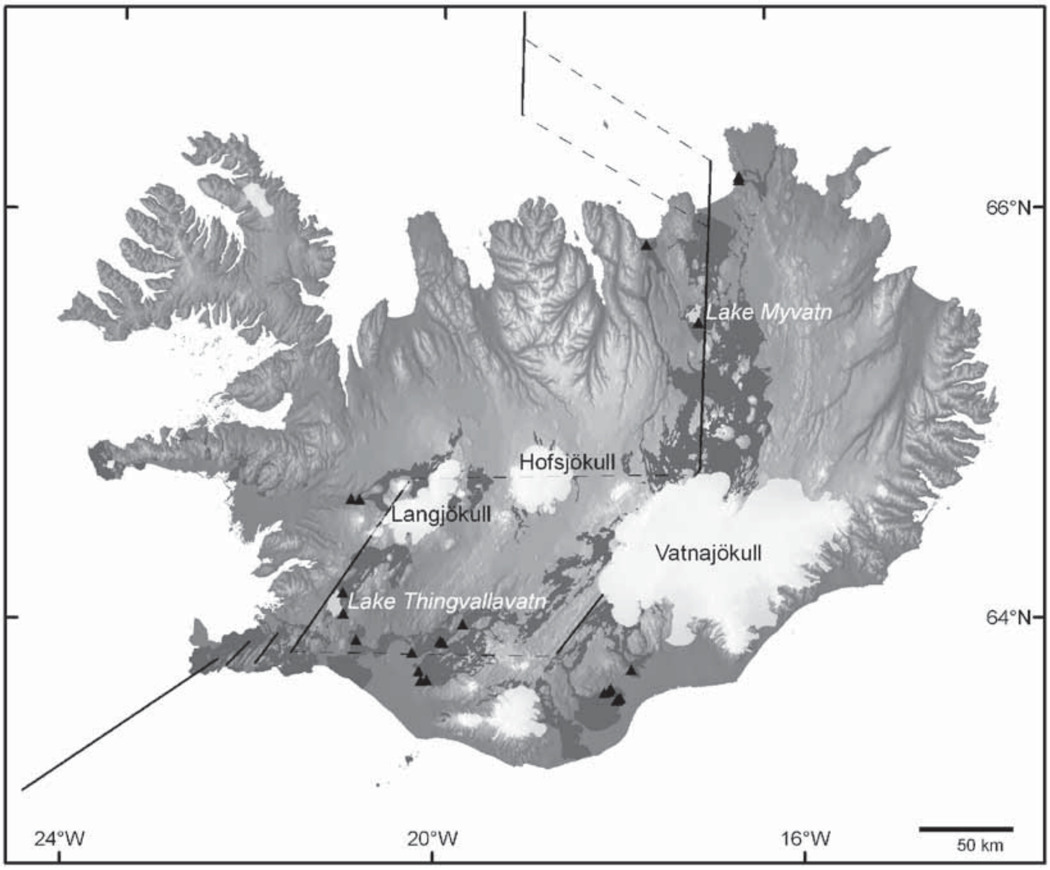

FIGURE 7. Sites with *C. islandicus* **sp. nov.** in Iceland. The large recent glaciers, i.e. Langjökull, Hofsjökull and Vatnajökull, are shown, as well as the large lakes, i.e. Lake Thingvallavatn and Lake Myvatn. Recent lava fields (since last glaciation; <18.000 years, shaded area) are shown as well as the plate boundaries. Source: Institute of Earth Sciences, University of Iceland.

Discussion

The limnic fauna of Iceland is fairly poor (Malmquist 1998) and less diverse than the continental limnic fauna to the east and to the west of Iceland. This is particularly true for

the fish fauna, which holds only a few salmonids (arctic charr, *S. alpinus*; brown trout, *Salmo trutta*; Atlantic salmon, *Salmo salar*), the three-spined stickleback (*Gasterosteus aculeatus*), the American and the European eels (*Anguilla anguilla* and *A. rostrata*) and the estuarine flounder (*Platichthys flesus*). The epigean limnic fauna has no endemic species. The low diversity and lack of endemism of the freshwater organisms, as with the terrestrial fauna and flora (Aegisdóttir & Thórhallsdóttir 2004), has been explained as a consequence of the young age of the fauna, which probably arrived after the last glaciations (Coope 1986; Sadler 1999). Some plant species may have survived on nunataks during later glacial epochs (Rundgren & Ingólfsson 1999). The arctic charr and the three-spined stickleback do show pronounced polymorphism in Iceland and in the Lake Thingvallavatn four morphs of the former species have been recognized, suggesting rapid speciation in the area (Kristjánsson *et al*. 2002). This radiation has partly been explained by plasticity of the species, and by an availability of a variety of unused habitats, including the heterogeneous lava fields.

A subterranean species has only recently been reported from subarctic Europe, i.e. from Iceland (Kristjánsson & Svavarsson 2004). A new species, belonging to a new amphipod family, Crymostygiidae Kristjánsson & Svavarsson, 2004, was recently discovered in the same spring outlet, Vatnsvik, as *C. islandicus* **sp. nov.** The presence of two subterranean amphipod species from two different families (Crymostygiidae and Crangonyctidae, respectively) in Icelandic subterranean waters may indicate that both these species have been present in this environment for a long time. Kristjánsson & Svavarsson (2004) suggested that the endemic *Crymostygius thingvallensis* survived the Pliocene and Pleistocene glaciations probably in groundwater flowing through the porous lava beneath the glaciers. Subglacial refugia have previously been suggested for species of the Crangonyctidae, i.e. for species of the genera *Stygobromus* and *Bactrurus* (Holsinger 1981, 1986; Koenemann & Holsinger 2001). Subglacial refugia may also have been the case for *Crangonyx richmondensis* Ellis, 1940 (Zhang & Holsinger 2003).

Iceland is unique in the North East Atlantic Ocean in having extensive volcanic activity, due to the presence of a hot spot (Iceland plume) at the plate boundaries beneath the island (Shen *et al.* 1998; Guðmundsson 2000; Torsvik *et al.* 2001). This activity is mainly on a northeast-southwest axis across the country, where extensive porous or permeable lava fields are located (Fig. 7). The porous lava field with extensive groundwater flow (see for instance Kiernan *et al.* 2003), often with large subterranean rivers, may have been important for sustaining populations of the subterranean species in Iceland, conditions probably not found at the continents to the west and the east of Iceland (Greenland and Scandinavia, respectively). All present reports of *C. islandicus* **sp. nov.** are within this active zone of Iceland. Groundwater springs are rare in North-western and Eastern Iceland. There the rock has been sealed and compacted by secondary mineralization.

Subterranean amphipods have been observed on many Atlantic islands (Stock 1993).

The origin of these amphipods has been traced to the opening of the Atlantic Ocean and the break up of the Tethys Sea. The occurrence of two stygobiont species in Iceland is particularly interesting in light of the age of the island and the fact that groundwater species occur on an Atlantic island, which has been covered by a glacier. Prior to the glaciations, ending only around 10 to 12 000 years ago (Geirsdóttir & Eiríksson 1994), Iceland had a warm climate. A Cfa climate (humid warm temperature with no dry season and hot summers) persisted in Iceland until at least 10 M years ago (Denk *et al*. 2005). Previously the early Tertiary flora has been considered to have close affinity with the recent flora of North America's Eastern Deciduous forests (Símonarson 1979). Older vegetation (= 12 M years old) and possibly also plants from 10 M years ago are now assumed to have originated from both Europe and North America, while plant assemblages from later dates (9–8 M years old) have been assumed to have originated from Europe (Denk *et al*. 2005). The occurrence of a fossil hickory aphid (6.7–16 M years old) in Icelandic, resembling *Longistigma caryae* Harris, 1841, currently living in North America indicates colonization from North America (Heie & Friedrich 1971). The occurrence of *Crangonyx islandicus* **sp. nov.** in Iceland, belonging to a family dominated by North American species, indicates that prior to the glaciations the species may have originally arrived from the west, i.e. from North America presumably via Greenland.

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References

Adalsteinsson, H., Jónasson, P.M. & Rist, S. (1992) Physical characteristics of Thingvallavatn, Iceland. *Oikos*, 64, 121–135.

Aegisdóttir, H.H. & Thórhallsdóttir, Th.E. (2004) Theories on migration and history of the North-Atlantic flora: a review. *Jökull*, 54, 1–16.

Arnason, B. (1976) Groundwater systems in Iceland traced by Deuterium. *Societas Scientarium Islandica, Occasional publications*, 42, 1–236.

Botosaneanu, L. (ed) (1986) *Stygofauna mundi. A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial)*. E.J. Brill, Leiden, 740 pp.

Coope, G.R. (1986) The invasion and colonization on the North Atlantic islands: a palaeoecological solution to a biogeographical problem. *Philosophical Transactions of the Royal Society of Lon-*

don, Series B, 314, 619–635.
Costello, M. (1993) Biogeography of alien amphipods occurring in Ireland, and interactions with native species. *Crustaceana*, 65, 287–299.
Denk, T., Grímsson, F. & Kvaček, Z. (2005) The Miocene floras of Iceland and their significance for late Cainozoic North Atlantic biogeography. *Botanical Journal of the Linnean Society*, 149, 369–417.
Einarsson, Á., Stefánsdóttir, G., Jóhannesson, H., Ólafsson, J.S., Gíslason, G.M., Wakana, I., Gudbergsson, G. & Gardarsson, A. (2004) The ecology of the Lake Myvatn and the River Laxá: Variation in space and time. *Aquatic Ecology*, 38, 317–348.
Geirsdóttir, Á. & Eiríksson, J. (1994) Growth of an intermittent ice sheet in Iceland during the late Pliocene and early Pleistocene. *Quaternary Research*, 42, 115–130.
Gíslason, S.R., Arnórsson, S. & Ármannsson, H. (1996) Chemical weathering of basalt in Southwest Iceland: Effects of runoff, age of rocks and vegetative/glacial cover. *American Journal of Science*, 296, 837–907.
Guðmundsson, Á. (2000) Dynamics of volcanic systems in Iceland; example of tectonism and volcanism at juxtaposed hot spot and mid-ocean ridge systems. *Annual Review of Earth and Planetary Sciences*, 28, 107–140.
Heie, O.E. & Friedrich, W.L. (1971) A fossil specimen of the North American Hickory Aphid (*Longistigma caryae* Harris), found in Tertiary deposits in Iceland. *Entomologica Scandinavica*, 2, 74–80.
Hjartarson, Á. (1988) The Þjórsá lava – the largest Holocene lava flow on Earth. *Náttúrufræðingurinn*, 58, 1–16 (in Icelandic).
Holsinger, J.R. (1977) A review of the systematics of the Holarctic amphipod family Crangonyctidae. *Crustaceana, supplement*, 4, 244–281.
Holsinger, J.R. (1981) *Stygobromus canadensis*, a troglobite amphipod crustacean from Castleguard Cave, with remarks on the concept of glacial refugia. *Proceedings of the 8th International Congress of Speleology*, 1, 93–95.
Holsinger, J.R. (1986) Zoogeographical patterns of North American subterranean amphipod crustaceans. *In*: Gore, R.H. & Heck, K.L. (eds.) Crustacean Biogeography. *Crustacean Issues*, 4, 85–106.
Holsinger, J.R. (1993) Biodiversity of subterranean amphipod crustaceans: global patterns and zoogeographic implications. *Journal of Natural History*, 27, 821–835.
Jakobsson, S. (1976) The age of the Grímsnes lavas, SW-Iceland. *Náttúrufræðingurinn*, 46, 153–162 (in Icelandic).
Jónsson, J. (1987) The Eldgjá eruption and the age of the Landbrot lava. *Náttúrufræðingurinn*, 57, 1–20 (in Icelandic).
Kiernan, K., Wood, C. & Middleton, G. (2003) Aquifer structure and contamination risk in lava flows: insights from Iceland and Australia. *Environmental Geology*, 43, 852–865.
Kikuchi, S., Matsumasa, M. & Yashima, Y. (1993) The ultrastructure of the sternal gills forming a striking contrast with the coxal gills in a fresh-water amphipod (Crustacea). *Tissue and Cell*, 25, 915–928.
Kjartansson, G. (1964) ^{14}C ages of some postglacial lavas in South-Iceland. *Náttúrufræðingurinn*, 34, 101–113 (in Icelandic).
Kristjánsson, B.K., Skúlason, S. & Noakes, D.L.G. (2002) Morphological segregation of Icelandic threespine stickleback (*Gasterosteus aculeatus* L.). *Biological Journal of the Linnean Society*, 76, 247–257.
Kristjánsson, B.K. & Svavarsson, J. (2004) Crymostygiidae, a new family of subterranean freshwater gammaridean amphipods (Crustacea) recorded from subartic Europe. *Journal of Natural History*, 38, 1881–1894.
Koenemann, S. & Holsinger, J.R. (2001) Systematics of the North American subterranean amphi-

pod genus *Bactrurus*. *Beaufortia*, 51(1), 1–56.
Larsen, G. (1979) Tephrochronological dating of the Eldgjá lavas in South-Iceland. *Náttúrufræðingurinn*, 49, 1–26 (in Icelandic).
Malmquist, H.J. (1998) Rivers and lakes in Iceland: Ecology and wetland interactions. *In*: Ólafsson, J.S. (Ed.). Icelandic wetlands. University Press, Reykjavík, pp. 37–55 (in Icelandic).
Rundgren, M. & Ingólfsson, Ó. (1999) Plant survival in Iceland during periods of glaciation? *Journal of Biogeography*, 26, 387–396.
Sadler, J.P. (1999) Biodiversity on oceanic islands: a palaeoecological assessment. *Journal of Biogeography*, 26, 75–87.
Shen, Y., Solomon, S.C., Bjarnason, I.Th. & Wolfe, C.J. (1998) Seismic evidence for a lower-mantle origin of the Iceland plume. *Nature*, 395, 62–65.
Símonarson, L. (1979) On climatic changes in Iceland. *Jökull*, 29, 44–46.
Sket, B. (1999) The nature of biodiversity in hypogean waters and how it is endangered. *Biodiversity and Conservation*, 8, 1319–1338.
Stock, J.H. (1993) Some remarkable distribution pattern in stygobiont Amphipoda. *Journal of Natural History*, 27, 807–819.
Sveinbjörnsdóttir, Á.E. & Johnsen, S.J. (1992) Stable isotope study of the Thingvallavatn area. Groundwater origin, age and evaporation models. *Oikos*, 64, 136–150.
Sæmundsson, K. (1992) Geology of the Thingvallavatn area. *Oikos*, 64, 40–68.
Torsvik, T.H, Mosar, J. & Eide, E.A. (2001) Cretaceous-Tertiary geodynamics; a North Atlantic exercise. *Geophysical Journal International*, 146, 850–866.
Zhang, J. & Holsinger, J.R. (2003) Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America. *Virginia Museum of Natural History, Memoir*, 6, 1–274.